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Energy Requirements for Growth in Relation to Sexual Size Dimorphism in Marsh Harrier *Circus aeruginosus* Nestlings

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ABSTRACT

Food consumption was measured in six female and seven male hand-raised marsh harrier (*Circus aeruginosus*) nestlings. Females consumed on average 4,321 g and males consumed 3,571 g of food during the nestling stage from 0 to 36 d. Total consumption until 56 d was 6,960 g and 5,822 g for females and males, respectively. On the basis of Fisher's sex ratio theory, this food intake ratio of 0.46 (intake male/[intake male + female]) would explain the observed male-biased fledging sex ratio of 55% males in marsh harrier broods. Growth, gross energy intake, and metabolizable energy intake were measured, along with metabolism of the nestlings, enabling us to determine energy allocation. The assimilation quotient ($Q = 0.72$) did not differ systematically between the sexes. Differences in metabolic rates between males and females at 15 and 30 d of age were fully attributable to the difference in body mass. Sexual size dimorphism in marsh harriers (female body mass around 60 d of age is 1.28 times greater than male mass) did not fully explain the difference in food intake between male and female nestlings: an analysis of energy requirements for growth and body mass in 16 avian species shows that energy intake was less than proportional to the average body mass at release. The data presented in this study are in agreement with Fisher's theory of inverse proportionality between the sex-specific ratios of energy requirements for growth and of offspring numbers in the marsh harrier population.

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Introduction

Fisher's (1930) theory on sex ratio postulates that the total parental investment in all male and in all female offspring should be equal at the population level. In species where the size at independence differs between sons and daughters, one would therefore expect a sex ratio biased in favour of the smaller sex. This expectation is based on the assumption that the larger sex would have larger total energy requirements for growth until independence. Despite the widespread sexual dimorphism among birds with parental care, well-documented deviations from a 1 : 1 sex ratio are rare (Clutton-Brock 1986; Gowaty 1993). In an extremely sexually dimorphic raptor like the sparrowhawk (*Accipiter nisus*), for instance, the sex ratio at fledging does not significantly deviate from parity (Newton and Marquiss 1979). In this species, field observations on food consumption of the nestlings have suggested that the heavier females do not require more food than the males (Newton 1978; but see Frumkin 1988). In contrast, food demand was related to sexual size dimorphism in several other studies (e.g., Fiala and Congdon 1983; Slagsvold et al. 1986; Anderson et al. 1993*b*). Since compensatory energy savings may balance the energetic costs for growth in the two sexes, it is important to obtain precise measurements of these costs under standard conditions.

In the marsh harrier, the female is the larger of the two sexes. In the Dutch population, males weigh on average 522 g and females weigh 743 g (C. Dijkstra, unpublished data). In this raptor a biased sex ratio at independence has been found (54.8% males; Zijlstra et al. 1992). While this bias is qualitatively expected from Fisher's theory, a quantitative evaluation requires assessment of the energy requirements for growth of sons and daughters throughout the phase of parental care. In this study, we have undertaken such a comparison. We raised 13 nestling marsh harriers (six females, seven males) by hand, from birth until 56 d of age, and quantified growth as well as energy intake, before release of the birds in the wild. We further evaluated energy expenditure of males and females by measuring oxygen consumption at two stages of growth. Finally, in order to estimate total food consumption until independence, we established the duration of parental care after fledging at six nests in nature. This allowed us to critically evaluate the prediction from Fisher's theory that total requirements of sons

should amount to 82% (i.e., 45.2/54.8) of the requirements of daughters.

Material and Methods

Animals and Housing

Eleven newborn marsh harrier nestlings and two starred eggs were collected from eight nests in our study area, the Lauwersmeer (53°20′ N 6°16′ E), in the second week of June 1992. Because of asynchronous hatching, last-born nestlings in large broods have a low probability of survival (Witkowski 1989; Zijlstra et al. 1992). For this reason we selected only last-born young from broods of at least four nestlings. Reproductive success was not affected detectably by taking young from a nest: fledging success (young fledged/clutch size) of nests where eggs were removed was 39% ($n = 8$ nests), compared to an average fledging success of 35% ($n = 23$ nests) in the remainder of the population in 1992 (B. Riedstra, personal communication).

The nestlings were placed in open plastic boxes (60 × 45 × 40 cm) provided with a layer of straw and cloth. Birds of the same age and of both sexes were placed together, five per box in the first 2 wk, four per box later on. Boxes were maintained in a temperature-controlled room (16L : 8D; lights on 0700 hours EET). After 1 wk at 32°C, temperature was gradually reduced to 23°C in the course of 2 wk. At 36 d of age, the birds were moved to an outdoor aviary (8 × 5 × 3 m). When all birds were 50 d of age or older (July 30), they were released in the Lauwersmeer area. In the following month, food (day-old cockerels and mice, occasional roadkills [rabbit and duck] found) was left at the release site every morning. The amount of food offered was gradually reduced to zero in the course of the month. Observations showed that at least seven of the 13 harriers made use of this food supply.

Growth

During the nestling phase, the following measurements were taken on all birds every day at 1330 hours, just after feeding: wing chord length, toe pad length (the maximum distance between the bases of the nails of toes 1 and 3), and head-bill length (maximum length from the tip of the bill to the back of the head). In the aviary, biometry of the birds was assessed once per week except for head-bill length and toe pad length, which were measured up to day 40, when their growth was completed. Body mass of each individual was assessed before and after each meal. For constructing the growth curves, body mass before the first meal in the morning was used. Gender was assessed using toe pad length. From an age of 20 d onward, toe pads differ significantly and without overlap between males and females (Zijlstra et al. 1992).

Food and Energy Intake

The harriers were fed five times per day, at 0730, 1030, 1330, 1630, and 1930 hours. Food consisted of dead day-old cockerels, of which the yolk was removed, because of the difference in energy content between yolk and meat, and since the precise amount of the fluid yolk consumed is difficult to establish. Twice a day a mixture of vitamins and minerals (Carnicon) was added. During the first 8 d the birds were fed with small pieces of chick without bones. From 9 to 15 d of age pieces of bone (limbs, ribs) were added. From day 16 onward the complete chick was offered, at first in larger pieces. From day 25 onward the birds were able to handle a chick themselves.

Until 36 d of age, gross food intake of the young was assessed by weighing the young before and after each meal. Droppings produced during meals were weighed and corrected for. Water content of the food was established by weighing and drying (2 d at 60°C) a sample of each meal. The water content varied between 71% and 80%. After day 35, food intake measurements were restricted to two consecutive days every 6 d and were carried out in a smaller cage, separated from the aviary by a meshed wire fence. Food was given to these birds three or four times a day, and remnants were removed after 2 h. The food intake was calculated by subtracting the remnants from the amount of food offered. The weight of the remnants was corrected for water loss. This was done by leaving a tray with food in a similar environment and weighing the decrease in mass. In the aviary, birds were trained to eat dead as well as live mice (*Mus musculus domesticus*) during one or two meals per day.

Assimilation quotients (Q) of isolated birds were assessed at ages 10, 17, and 24 d. Each bird was isolated for approximately 24 h, from one morning until the next. All faeces and pellets produced in 1 d were collected. Energy content of food, faeces, and pellet samples was measured by bomb calorimetry. All pellets and faeces produced during the isolation were measured, as well as four samples of food offered at different ages. The energy equivalents were used to calculate gross energy intake (I, kJ d^{-1}) and metabolizable energy intake (M, kJ d^{-1}) from food intake rates. The assimilation quotient Q equals M/I.

Metabolic Rate

Oxygen consumption was measured in four females and five males of 15 d old, and in each bird at the age of 30 d. The measurement at the age of 15 and 30 d was done overnight, in a darkened room, from 1900 to 0930 hours. The birds were placed in an air-proof Perspex chamber of approximately 15 and 30 L (for birds of 15 and 30 d, respectively) at 25°C. Dried air was pumped through the respiration chamber at a flow rate of approximately 100 L h^{-1} at 15 d old up to 150 L h^{-1} at 30 d old. Oxygen concentration of the inlet and outlet air was

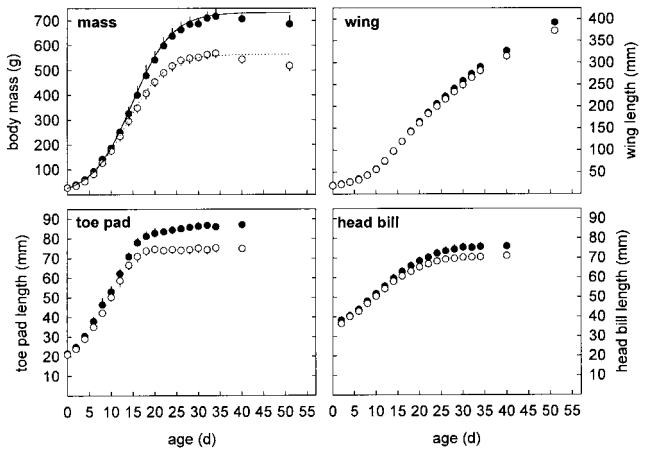

Figure 1. Growth of body mass (measured in the morning), wing, toe pad, and head bill of male (*open circles; n* = 7) and female (*filled circles; n* = 6) nestlings, given with standard deviations and at 2-d intervals. Lines in mass graph represent mass of male (*dotted line*) and female (*solid line*) nestlings under natural conditions (Riedstra et al. 1998).

measured at 1-min intervals. Rates of oxygen consumption were converted to energy expenditure using an energetic equivalent of 19.8 kJ L^{-1} O_2 (assuming a respiratory quotient of 0.72; Gessaman and Nagy 1988). The average nocturnal energy expenditure (*E*) obtained from these measurements are expressed in kJ d^{-1}. For details of the experimental setup, see Meerlo et al. (1997). At 30 d of age the measurement was continued until ca. 1600 hours. In this case the light was switched on at 0700 hours, and the birds received a tray with a known amount of food (±100 g) at 1100 hours.

Duration of Postfledging Care

To estimate the duration of postfledging care, observations were made in the Lauwersmeer study area in August on six nests, each with at least one male and one female fledgling. All nestlings had coloured wing tags, to enable individual recognition. Hatching dates of first chicks fell between June 2 and 17. Observations were made in 7-d intervals and varied between ages 47 and 90 d of the fledglings. Each observation lasted 3 h or more and was made from a distance of more than 200 m from the nest. The number of observed prey deliveries by male and female parents to each individual offspring was recorded.

Results

Growth

Figure 1 shows the development of male and female body mass. From the age of 12 d onward, body mass differed significantly between the sexes (day 12: $t_{11} = 2.57$, $P < 0.05$). At approximately 35 d of age, body mass reached its maximum, where females (718 g) were 1.26 times heavier than males (569 g). At this age, around which nestlings normally fledge (Glutz von Blotzheim et al. 1971), the birds were moved to the aviary. In the following days, body mass decreased slightly. Asymptotic body mass, growth constant, inflection point, and coefficient of determination are given in Table 1. Growth of the harriers in the lab is similar to growth measured on harrier nestlings in the field (Riedstra et al. 1998). However, body mass in the field was measured throughout the day, whereas the lab data shown represent body mass in the morning before the first meal. This implies that body mass of the harriers raised in the lab was in fact slightly higher than that of free-living harriers.

Wings (Fig. 1) developed more slowly than body mass, head-bill length, and toe pad length. Average wing length of 51-d-old females was only 1.05 times that of males, and the difference between the sexes was not significant at any age. Asymptotic length of the wings as calculated by curve fitting underestimates true asymptotic length, because of the nature of the growth of the wing. Fitting a logistic growth curve through the available data did give an estimate of the growth constant and the inflection point (Table 1). Toe pad length differed between males and females from the age of 4 d onward (Fig. 1; Table 1). When fully grown, female toe pad length was 1.15 times larger than male toe pad length. The toe pads reached their final length in a relatively short time. Head-bill length (Fig. 1; Table 1) reached its final size as early as around 25 d of age. The difference between male and female head-bill length was significant from 16 d of age onward (day 16: $t_{11} = 3.02$, $P < 0.05$), but the difference was small: when full grown, head-bill length of the female was 1.07 times greater than of the male.

Figure 2 shows the daily growth rates of male and female nestlings as a function of age (*A*) and body mass (*B*). Maximum growth rate was 39.2 g d^{-1} (SD = 2.9, $n = 6$) in females, and 30.4 g d^{-1} (SD = 2.5, $n = 7$) in males, which is significantly lower ($t_{11} = 5.88$, $P < 0.001$). Males reached maximum growth rate earlier than females (Fig. 2*A;* $t_{11} = 2.60$, $P < 0.05$; females: 14.7 d, SD = 2.1, $n = 6$; males: 12.0 d, SD = 1.6, $n = 7$) and at a lower body mass (Fig. 2*B;* $t_{11} = 4.09$, $P < 0.005$; females: 349.4 g, SD = 55.9, $n = 6$; males: 236.1 g, SD = 44.1, $n = 7$).

Food Intake

Average daily food intake of females exceeded that of males during most of the nestling period (Fig. 3). Only during the first 10 d of age, when the size difference between the sexes was small, were food intake rates not statistically distinguishable. Mean maximum food intake was 192.8 g d^{-1} (SD = 10.3; $n = 6$) for females, and 158.1 g d^{-1} (SD = 9.5; $n = 7$) for males. The age at which maximum food intake was reached did not differ significantly between male and female nestlings ($t_{11} = 0.44$; females: 23.7 d, SD = 4.3, $n = 6$; males: 22.9 d,

Table 1: Asymptotic size (A), growth constant (k), inflection point (t_i, days), and coefficient of determination (r^2) of body mass, toe pad length, wing length, and head-bill length

	Females				Males			
	A	k	t_i	r^2	A	k	t_i	r^2
Body mass (g):								
Average	714.5	.22	14.8	.992	558.9	.24	13.5	.988
SD	23.34	.015	.72	.004	17.65	.012	.52	.003
Toe pad length (mm):								
Average	87.6	.21	7.2	.993	76.2	.24	6.5	.986
SD	1.64	.013	.67	.005	2.08	.017	.29	.004
Wing length (mm):								
Average	387.4	.12	23.7	.993	370.3	.12	23.0	.992
SD	9.71	.005	.94	.002	5.48	.003	.30	.002
Head-bill length (mm):								
Average	78.2	.12	4.1	.997	72.5	.13	3.4	.996
SD	2.33	.014	.67	.002	1.13	.007	.46	.002

Note. A, k, t_i, and r^2 were determined with logistic curve fitting. Asymptote of wing is not the adult wing length but the asymptote of the nestling as determined by curve fitting. Data show the averages of six females and seven males, with standard deviations, after individual curve fitting.

SD = 2.0, $n = 7$) and was considerably later than the age of maximum growth rate (Fig. 2; 14.7 d for females; 12.0 d for males).

From day 0 until day 36, the nestling period, total food intake was on average 4,321 g per female (SD = 259, $n = 6$) and 3,571 g per male (SD = 138, $n = 7$). This difference is significant ($t_{11} = 6.67$, $P < 0.001$). A female would thus be 1.21 times more expensive to raise than a male, if only the nestling stage were taken into account.

In order to estimate the total food intake of the young, the whole period of parental care should be taken into consideration. From observations (see *Duration and Intensity of Parental Care*) it was established that the parents on average feed their young through the age of 69 d. The amount of food the harriers consumed during the postfledging period was estimated by extrapolating the mean amount of food eaten in the period during which the birds were in the aviary (from 36 until on average 56 d of age). The total food intake of the young, from day 0 through day 69, could then be estimated as 8,675 g (SD = 426, $n = 6$) per female and 7,286 g (SD = 535, $n = 7$) per male. Again, the difference is significant ($t_{11} = 5.11$, $P < 0.0005$). Thus, a female would be 1.19 times more expensive to raise than a male. The food ratio (i.e., the fraction of food going to the male of a male-female unit) would be 0.456 in 69 d of laboratory raising (see also Table 2). We could not demonstrate a significant difference between the ages at which male and female chicks fledge, possibly because of small sample sizes. However, if the observed fledging ages of males and females are taken into account separately, the food intake over the entire period of parental care is greatly influenced. In the most extreme case, in which mean age of all male and female chicks is calculated separately rather than grouped per nest, estimated total food consumption of females is 9,071 g (SD = 457, $n = 6$) over 72 d (SD = 6.4, $n = 7$), and that of males is 7,173 g (SD = 522, $n = 7$) over 68 d (SD = 6.5, $n = 10$). This gives a food consumption that is 1.26 times higher in males than in females. See Table 2 for a summary of the food intake data.

Metabolizable Energy

The energy content of the food offered at ages 0–8 d (cockerel meat, no bones) was 26.2 kJ g dry^{-1} (SD = 0.1, $n = 4$), at age 9–15 d (cockerel pieces) was 25.8 kJ g dry^{-1} (SD = 0.6, $n = 4$) and at age >15 d (whole cockerels) 26.8 kJ g dry^{-1} (SD = 2.4, $n = 4$). The differences in energy content between the three food types are negligible, and gross energy intake (I, kJ d^{-1}) was calculated by multiplying the dry food intake with the average energy content of the food, as indicated in Figure 3.

From the assimilation data, the metabolizable energy intake (M) could be calculated by subtracting the energy excreted in pellets and faeces from I. Assimilation quotients ($Q = M/I$) of male and female nestlings were statistically indistinguishable between the three ages (Table 3). Mean Q was 0.72 (SD = 0.08, $n = 28$). This assimilation quotient is slightly less than the average value of 0.79 found in other raptors fed day-old cockerels (Castro et al. 1989; Barton and Houston 1993). This may be partly due to the exclusion of egg yolk from the diet we offered.

In Figure 4 the estimated values of metabolizable energy intake are plotted as a function of body mass. For comparison,

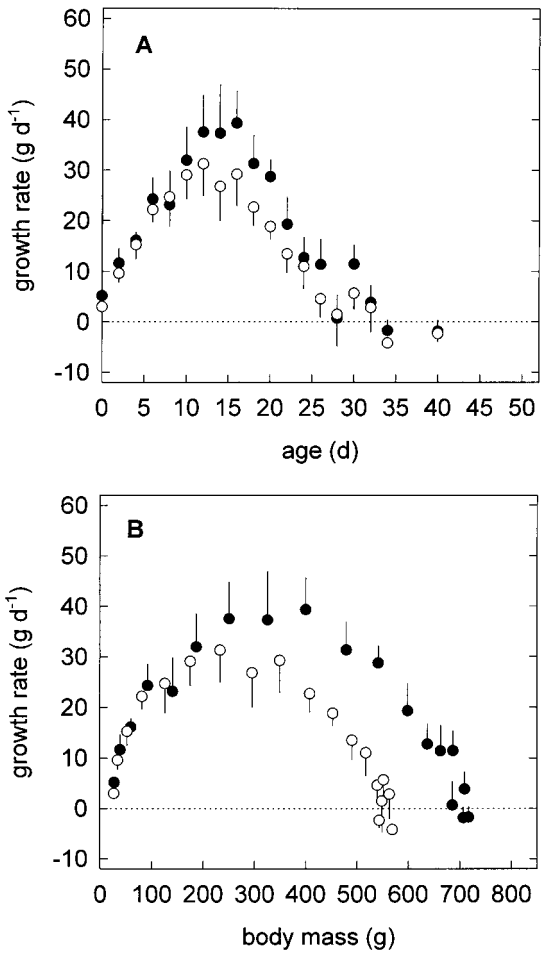

Figure 2. Growth rate of male (*open circles; n* = 7) and female (*filled circles; n* = 6) nestlings, plotted against age (*A*) and body mass (*B*). Data are shown with standard deviations and give an average over 2 d.

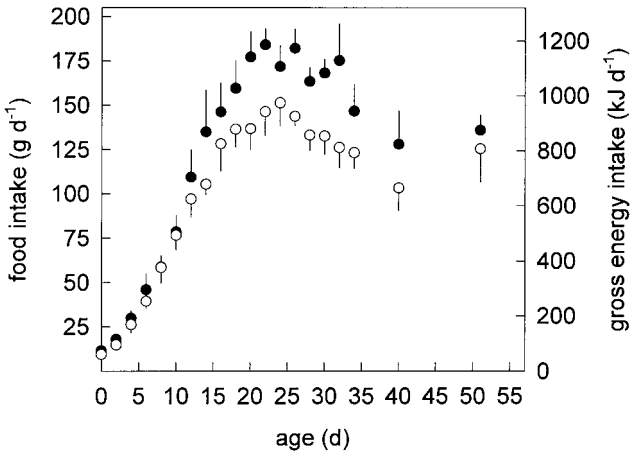

Figure 3. Daily food intake of male (*open circles*) and female (*filled circles*) nestlings with standard deviations, shown as a function of age. Gross energy intake is scaled on the right axis.

Table 2: Mean amount of food consumed by seven male and six female nestlings (with standard deviations) and food intake ratios, during the nestling stage (age 0–36 d), during the fledgling stage (36–56 d), and total consumption until 56 d of age (0–56 d)

	Food Intake[a] (g)		
Period (d)	Female	Male	Food Ratio[b]
0–36	4,321 (259)	3,571 (138)	.452
36–56	2,639 (249)	2,251 (265)	.460
0–56	6,960 (311)	5,822 (368)	.456

[a] Data are means; SDs are given in parentheses.
[b] Food ratio = (male/[male + female]).

the allometric interspecies equation for maximal adult metabolizable energy intake (from Kirkwood [1983]: $M = 1{,}713$ (body mass)$^{0.72}$ kJ d^{-1} [body mass in kilograms]) was drawn. Initially, the energy intake of growing marsh harriers was lower than the predicted maximum, but this adult level is indeed approached as the birds grow older.

Metabolic Rate

Nocturnal energy expenditure (*E*), at ages 15 and 30 d, respectively, was for females on average 246 kJ d^{-1} (SD = 45.7, $n = 4$) and 385 kJ d^{-1} (SD = 81.9, $n = 6$), and for males 207 kJ d^{-1} (SD = 7.2, $n = 4$) and 310 kJ d^{-1} (SD = 60.4, $n = 7$). *E* increased with body mass, with mass explaining 65% of the variance observed ($P < 0.001$, $n = 21$; Fig. 5). When mass was taken into account, neither sex nor age of the nestlings had a significant effect on the metabolic rate.

Figure 6 combines our estimates for metabolizable energy intake (*M*, calculated as $I \times Q$) and the nocturnal rate of energy expenditure. The metabolism measurements during daytime at the age of 30 d suggested that diurnal rate of *E* of fed nestlings exceeded the nocturnal rates by on average 19.2% (SD = 19.4, $n = 13$). This would lead to a total energy expenditure of 416 kJ d^{-1} (females) and 327 kJ d^{-1} (males), leaving 372 kJ d^{-1} (females) and 294 kJ d^{-1} (males) for storage in growing tissues.

Duration and Intensity of Parental Care

At the end of the breeding season seven female and 10 male fledglings from six nests were observed. The mean age at which parental care stopped was 69 d (SD = 6.0, $n = 6$), and did not differ significantly between male and female fledglings (females: 71 d, SD = 5.4, $n = 6$; males: 68 d, SD = 7.4, $n = 6$; paired *t*-test).

During the field observations, the number of prey deliveries from both parents to male and to female fledglings was observed. Broods are fed as a unit: as long as parents deliver prey,

Table 3: Amounts of energy (with SDs) entering and leaving the bodies of male and female nestlings at the ages of 10, 17, and 24 d

	Females			Males		
	10 d	17 d	24 d	10 d	17 d	24 d
Intake:						
g fresh	77 (10)	165 (17)	174 (17)	71 (13)	135 (19)	151 (17)
kJ	497 (92)	1,043 (177)	1,090 (156)	460 (76)	882 (182)	940 (160)
n	6	6	6	7	7	7
Faeces:						
g dry	6.8 (.2)	9.4 (2.4)	12 (1.5)	4.5 (.7)	7.3 (1.1)	11 (1.6)
kJ g dry^{-1}	16 (1.6)	15 (1.3)	14 (1.4)	15 (.9)	14 (1.3)	14 (1.2)
kJ	111 (7.4)	142 (38)	172 (19)	67 (11)	105 (21)	151 (25)
n	3	6	6	3	7	7
Pellets:						
g dry	3.1 (1.1)	5.0 (2.3)	4.4 (1.1)	3.2 (1.0)	4.7 (1.8)	5.0 (2.0)
kJ g dry^{-1}	27 (1.1)	25 (.3)	24 (.3)	26 (.9)	24 (.5)	24 (2.1)
kJ	84 (34)	126 (58)	105 (23)	85 (29)	114 (44)	120 (55)
n	2	5	4	7	7	7
M:						
kJ	360 (125)	726 (142)	861 (124)	311 (96)	663 (181)	669 (195)
n	2	5	4	3	7	7
Q	.64 (.12)	.72 (.08)	.75 (.02)	.66 (.10)	.74 (.07)	.70 (.10)
n	2	5	4	3	7	7

Note. Food consumed (intake, g fresh) was converted into gross energy intake (*I*, kJ) using the caloric content of the food (see text). Energy leaving the body with the excrements (kJ produced) was calculated by measuring amount of pellets and faeces produced (g dry produced) and the caloric contents of the excrements (kJ g dry^{-1}). Metabolizable energy intake (*M*, kJ) = *I* − kJ excreted. Assimilation quotient (*Q*) = *M*/*I*. Sample sizes are given below each group of data.

both sexes take their share. Older nestlings can claim an entire prey, and when the chicks are able to fly, prey transfers from parent to fledgling take place in the air. Seven female fledglings together received 18 prey items (i.e., 2.6 prey per female), while 10 males together received 16 prey items (i.e., 1.7 prey per male) during 150 h of observation. On eight prey deliveries it could not be established which gender obtained the prey. The majority of the prey was delivered by the father (74%). We have no evidence that there was a difference in the rate of prey transfer to sons and to daughters (Table 4).

Discussion

The total food intake, integrated over 56 d of development until release in the wild was on average 6,960 g for female marsh harriers and 5,822 g for males, a ratio of 1.20. This is slightly less than proportional to the average mass at release (ratio 1.28; Table 1). Body mass of our hand-reared nestlings did not deviate from that of wild nestlings (Riedstra et al. 1998), although it is likely that there has been a slight difference since our hand-reared nestlings were weighed early in the morning, while wild nestling weights were taken throughout the day. Adult marsh harriers captured during the breeding season in the Netherlands had an average body mass of 743 g (SD = 53; $n = 15$) in females and of 522 g (SD = 36; $n = 30$) in males, respectively, representing a mass ratio of 1.42 (unpublished data from our lab). This higher ratio is probably due to fat deposition in females during the breeding season. For a comparison between food requirements and body mass it appears therefore that mass at independence gives a better estimate than adult body mass. The average assimilation quotient ($Q = 0.72$) was not different between the sexes. Food intake ratio and energy intake ratio between the sexes can therefore be considered equivalent.

We address two questions concerning these data. First, to what extent do the intake data reflect the energy required for development in nature? And second, is it generally true among birds that the mass ratio of the two genders overestimates the ratio of their energy requirements for growth?

Obviously, energy requirements in the lab may differ from those in the field situation. The energetic costs for growth itself may have been similar to the natural situation, but other costs may differ between hand-reared and wild nestlings. How sexual size dimorphism affects natural daily energy expenditure of nestlings may depend on several factors, ranging from sibling aggression and hatching rank to activity and thermoregulation

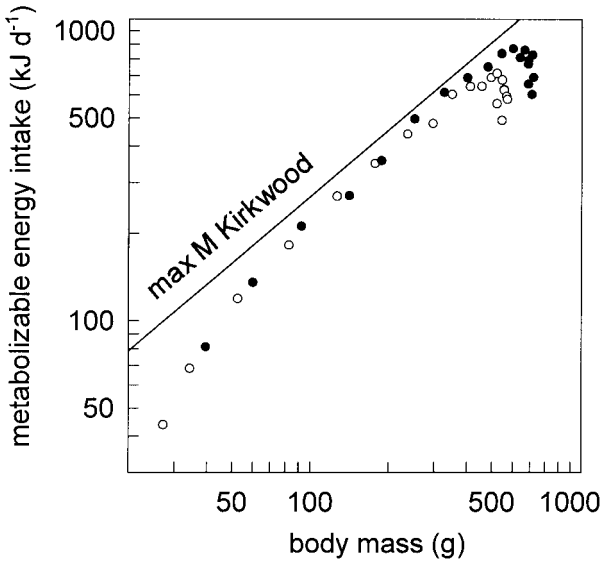

Figure 4. Metabolizable energy intake (M) of male (*open circles*) and female (*filled circles*) nestlings, at ages from 0 to 50 d, shown as a function of body mass. M was estimated from gross energy intake using the assimilation quotient. For comparison, maximum M as predicted by Kirkwood (1983; $M = 1{,}713\ \text{mass}^{0.72}$ [mass in kilograms]) is shown as well (*line*).

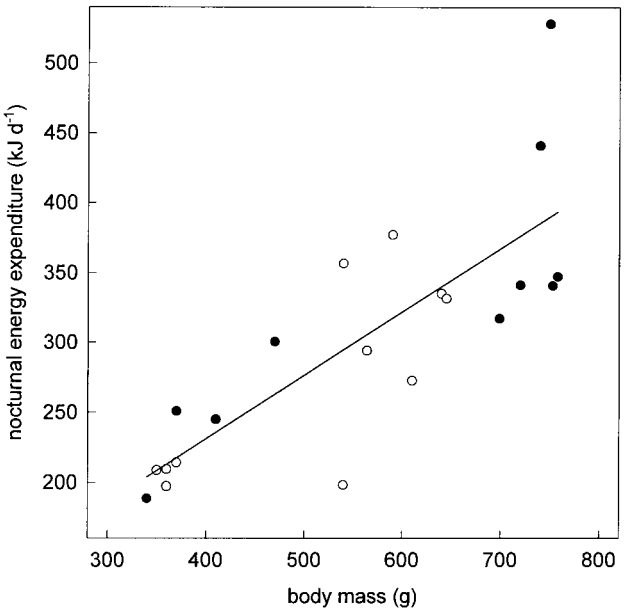

Figure 5. Nocturnal energy expenditure of male (*open circles; n = 7*) and female (*filled circles; n = 6*) nestlings, shown in relation to body mass. Body mass explains 65% of the variation in energy expenditure. Values below 500 g represent nestlings of 15 d of age; those above 500 g represent nestlings of 30 d. The line shows the linear regression: $y = 0.453x + 49.76$, $r^2 = 0.65$, $n = 21$.

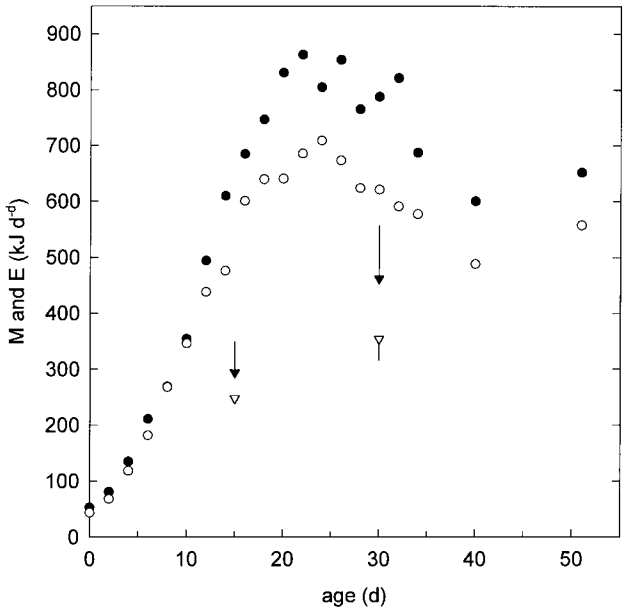

Figure 6. Comparison of metabolizable energy intake (*M; open circles,* male; *filled circles,* female) and estimated diurnal energy expenditure (*E; open triangles,* male; *filled triangles,* female) with standard deviation, of males and females, as a function of age. The range between M and E indicates the amount of energy available for storage in growing tissue.

(Cronmiller and Thompson 1981; Bortolotti 1986; Drummond et al. 1991; Richner 1991; Anderson et al. 1993*a*). It has been suggested that in some raptor species males show a higher degree of activity (Newton 1978; Frumkin 1988). This higher activity would increase the amount of energy required by males. However, in a study of free-living marsh harrier nestlings, Riedstra et al. (1998) assessed the energy expenditure by means of the doubly labeled water technique, and calculated that metabolizable energy intake (M) was 3.2% lower in males and 0.7% higher in females compared to intake rates of the hand-raised nestlings in the present study. Thus, the energetic re-

Table 4: Average number of delivered prey per hour per nestling, divided for male and female nestlings

	Number of Prey Received by	
Age (d)	Males	Females
51–55	.83	.33
56–60	.31	.03
61–65	.22	.66
66–70	.08	.11

Note. A distinction was made between five different age classes, ranging from 51 to 70 d of age.

quirements in the lab were indeed close to those in the field and do not suggest that differential costs of activity have played a significant role.

Under natural conditions, the difference in food consumption between male and female offspring may be compensated for if the male is fed for a longer time. However, we found no significant difference between males and females in the total duration of parental care, leaving no indication that this duration has an effect on the food ratio.

In this study we measured the energy required by nestlings for growth. The energy ratio for males and females presumably reflects the energy invested by the parents in male and female offspring, since the costs of capturing prey of a particular size should not vary between those which are fed to daughters and to sons. Only if the sons and daughters would receive prey of different size and if the costs of procuring such prey are not proportional to their mass, then slight deviations between energy requirement and energy investment ratios might be expected. A parent raising a single daughter (or son) has to invest energy in foraging in proportion to the energy requirement of the daughter (or son). In mixed broods there might be complications (e.g., due to competition) leading to an alteration of this proportionality. However, in the marsh harrier, field data on chick energy expenditure in mixed broods (Riedstra et al. 1998) closely reflect those obtained in the lab and thus do not suggest that the natural situation is basically different from the lab. Even if energy investment ratios could be precisely quantified, these would not include other energetic costs involved in reproduction. Hence, we consider the ratio of energy requirements as the best measurable reflection of investment.

Maximum growth rate was higher in females (39.2 g d^{-1}) than in males (30.4 g d^{-1}). This difference can be explained by the difference in body mass. Figure 2 shows that growth increases similarly in males and in females until the male body mass levels off. Thus it confirms Richner's (1991) conclusion that sex-specific growth dynamics do not equalize sex differences in energy requirements. Hence there is no implication for a response to sibling competition by faster growth in male nestlings, as was also observed by Schaadt and Bird (1993). We therefore have no reason to doubt that the data obtained in our study provide a reasonable estimate of the food ratio of the genders in the natural condition.

If one gender suffers a higher mortality before the end of parental care, this will affect the sex ratio, and also the relative cost of both sexes (see, e.g., Howe 1977; Richter 1983; Røskaft and Slagsvold 1985; Stamps 1990). Sex-dependent mortality probably does occur in the marsh harrier (Dijkstra and Daan 1998). This would increase the actual costs of raising female offspring if averaged over all females born, but not when averaged over all females raised, which is what Fisher's theory refers to.

A few other studies have addressed the question whether food requirements for growth differ between the genders of sexually dimorphic birds and summarized data from several species. Newgrain et al. (1993) measured crude growth efficiency in seven raptor species, which enabled them to predict total food intake (in grams) on the basis of body mass (in grams) by the equation: food intake = $20.54(\text{body mass})^{0.813}$. They did not test for proportionality, that is, whether the body mass exponent (0.813) significantly deviates from 1.0. Anderson et al. (1993*b*) reviewed 11 studies on this subject and reported a statistically significant association between the sexual dimorphism in body mass and the dimorphism in energy requirements for growth. Making use of the data provided and summarized by Anderson et al. (1993*b*) and Newgrain et al. (1993), we are now in a position to evaluate whether indeed the ratio of sex-specific energy requirements for growth is proportional to the ratio of sex-specific adult body mass. The database is presented in Table 5. This table includes 16 species: those two of Newgrain et al. (1993) where the food intake was measured on at least two individuals of each sex, the 11 species reviewed by Anderson et al. (1993*b*), and, in addition, the marsh harrier data reported here, recent data on the great blue heron (Bennett et al. 1995), and unpublished data for the European kestrel from our lab. For the analysis, we calculated the mass ratio R_m (male/female) and the food ratio R_f (male/female) and plotted these against each other (Fig. 7). The analysis confirms the positive association between R_m and R_f. The resulting regression is $R_f = 0.484 + 0.558R_m$ ($n = 16$; coefficient of determination $r^2 = 0.830$; standard error of intercept = 0.073, $P < 0.0001$; standard error of coefficient = 0.067, $P < 0.0001$). The 95% confidence interval of the coefficient is 0.413–0.702. Deriving the logarithms of the ratios gave a similar result (regression: $\log R_f = 0.022 + 0.520\log R_m$; coefficient of determination $r^2 = 0.821$; standard error of intercept = 0.009, $P < 0.05$; standard error of coefficient = 0.065, $P < 0.0001$; 95% confidence interval of the coefficient = 0.381–0.659). This shows that the relationship deviates sharply from proportionality. The regression slope is shallower than 1.0, and extreme body mass ratios overestimate the ratio in food requirements of the sexes. This implies that within each species the larger sex tends to be cheaper to raise on a per gram base than the smaller sex. This is in contrast to the observed interspecific allometric scaling exponent of 1.06 for the relationship between total metabolized energy intake and the body mass at fledging (Weathers 1992).

The food requirement ratio (male/female) is equivalent with a fractional cost (male/[male + female]) of 0.46. If this represents the relative cost to marsh harrier parents of raising a son, Fisher's theory would predict an optimal population sex ratio of fledglings reported for the Dutch population of 0.54. The sex ratio of fledglings reported for the Dutch population is 0.55 (Zijlstra et al. 1992). To judge whether this correspondence is accidental awaits evaluation in other species. The data presented in this study are in agreement with Fisher's theory of

Table 5: Male fraction (male/[male + female]) of body mass and food requirement ratio (male/[male + female]) of 16 bird species

Species	Male Fraction		Source
	Mass	Food	
Sparrow hawk (*Accipiter nisus*)	.341	.452	Frumkin 1988
Peregrine (*Falco peregrinus*)	.420	.446	Newgrain et al. 1993
Marsh harrier (*Circus aeruginosus*)	.413	.456	This study
Golden eagle (*Aquila chrysaetos*)	.455	.465	Collopy 1986
Australian kestrel (*Falco cenchroides*)	.454	.506	Newgrain et al. 1993
American kestrel (*Falco sparverius*)	.467	.483	Anderson et al. 1993*b*
Eurasian kestrel (*Falco tinnunculus*)	.463	.491	Unpublished data
Eastern bluebird (*Siala sialis*)	.504	.518	Droge et al. 1991
Pekin duck (*Anas platyrhynchos*)	.524	.507	Anderson et al. 1993*b*
Rook (*Corvus frugilegus*)	.465	.521	Slagsvold et al. 1986
Broiler chicken (*Gallus domesticus*)	.556	.545	Anderson et al. 1993*b*
Red-winged blackbird (*Agelaius phoeniceus*)	.573	.560	Fiala and Congdon 1983
Capercaillie (*Tetrao urogallus*)	.575	.573	Lindén 1981
Great-tailed grackle (*Quiscalus mexicanus*)	.612	.546	Teather and Weatherhead 1988:
Turkey (*Meleagris gallopavo*)	.612	.593	Anderson et al. 1993*b*
Great blue egret (*Ardea heroidas*)	.531	.515	Bennett et al. 1995

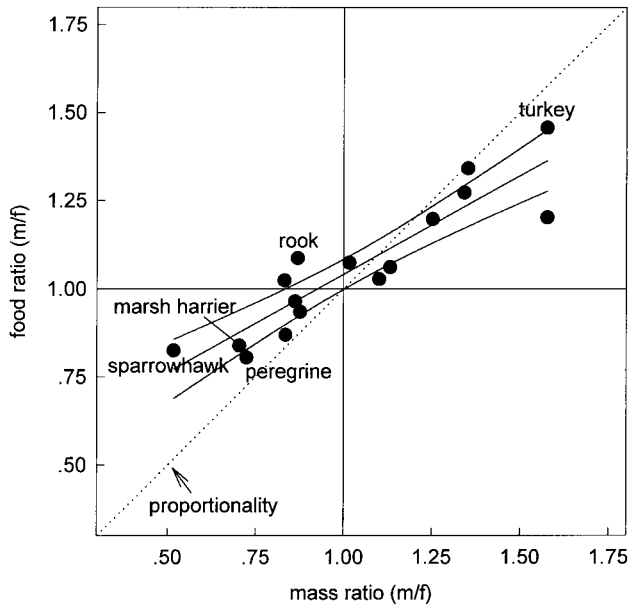

Figure 7. Relation between food ratio (intake male/intake female) and mass ratio (mass male/mass female) for 16 different species. See Table 5 for an explanation of data points. Solid lines show regression ($y = 0.484 + 0.558x$; $r^2 = 0.830$) and upper and lower 95% confidence intervals; dotted line shows proportionate relation between food and mass ratio.

inverse proportionality between the sex-specific ratios of energy requirements for growth and of offspring numbers in the population.

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